11. The Comparative Anatomy of the Tongues of the Mammalia. — VIII. Carnivora.

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[Received November 20, 1922 : Read March 6, 1923.]

(Text-figures 15–24.)

Contents.

Introduction.

The materials on which the present paper is based consisted of preserved and fresh specimens in the Society's Prosectorium and the Museum of the Royal College of Surgeons. Nearly five hundred tongues, representative of most genera were examined. Characters were observed which are of considerable value for purposes of classification, and a systematic arrangement of the tongues of the Felidæ, based on these features, agrees closely with Pocock's system (**24**), which was founded on external and cranial characters. It will be seen that the tongues differ from those described in my papers on the Primates (**29**), Ungulata, Sirenia, and Cetacea (**30**). Speaking generally the mechanical power is frequently greater and the gustatory organs are fewer than in many animals already described. The conical papillæ have strong, horny sheaths.

The tongues of the Fissipedia differ in many respects from those of the Pinnipedia.

Suborder FISSIPEDIA.

Section Æluroidea.

The tongue is long and comparatively narrow in all species, but it is wider in *Felis leo*, *F. tigris*, and *F. onca* than in other cats. It thickens progressively from before backwards, but the free part is never very thick. The sides are parallel or tapering, but the tongue is spatular in a few cases. The *apex* is truncated or rounded, but it is usually devoid of a notch. It is beset with

small conical and fungiform papillæ, but these do not stand up prominently. And there is in no case a large cluster of prominent fungiform papillæ containing large taste-buds, such as are present in the Primates. The *lateral borders* are rounded, but lateral organs are variable. They have many backwardly-directed conical papillæ; these usually lie flat in the Felidæ, but they stand up prominently in some of the Viverridæ. No lobules are present such as occur in the Cetacea.

The oral and pharyngeal parts of the tongue can be easily distinguished from one another when the vallate papillæ form a V or a triangle, and when there is a marked contrast between their conical papillæ. It is, however, difficult to distinguish them when the vallate papillæ form rows which do not meet, and when the conical papillæ maintain the same characters from the apex back to the epiglottis. The papillose base of the tongue is close to the epiglottis in all Æluroidea except *Felis leo* and *F. onca*, in which an extensive, smooth tract of mucous membrane intervenes between the base of the tongue and the epiglottis.

The conical papillæ in the Felidæ, Hyænidæ, and *Proteles*, have thick, sharp or rounded, horny sheaths, which can exert a powerful mechanical action on the food. This character is less marked in many of the Viverridæ. In some of the papillæ in *Proteles cristatus* they form blunt caps for rounded papillæ (text-fig. 21).

Median dorsal sulci and transverse dorsal ridges and sulci are absent. And there is no trace of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum.

Circumvallate Papillæ (text-fig. 15). The following patterns are present:—

1. A pair of papillæ.
2. Two or more pairs of papillæ arranged in converging rows, which do not meet in an apical papilla.
3. Three papillæ in a triangle with the apex behind.
4. Several papillæ in V-formation.
5. Papillæ form a double V.

The converging rows and the V can be regarded as incomplete or complete chevrons. There is no trace of T or Y types, or of fields of papillæ. And in no case were papillæ absent. It will be seen that pairs of papillæ are present in the Felidæ, Hyænidæ, and *Proteles*, but all types exist in the Viverridæ. As some tongues have no lateral organs, and few fungiform papillæ with taste-buds, the vallate papillæ are frequently the main gustatory organs.

It may be difficult to count the number of papillæ, for they are sometimes very small and inconspicuous, or concealed by overhanging conical papillæ. They may be all equal or unequal in size. They are circular, oval or dumbbell-shaped when viewed from above, and they are cylindrical or conical on elevation. One or more may be included in one fossa. The vallum and

fossa vary in prominence, and the papillary surface is smooth, finely granular or papillated. In the Felidæ, Protelidæ, and Hyænidæ there are one or more pairs of papillæ in rows which converge, but do not meet. In the Viverridæ there are in

Text-figure 15.

The circumvallate papillæ; *a–k*: papillæ on plan; *l*: papillæ on elevation.

addition to this pattern three papillæ in a triangle, or several papillæ in a single or double V.

The arrangements seen by myself and recorded by others are:—

Family Felidæ.

Felis leo:—One to five pairs of papillæ; seven papillæ in two rows.

F. tigris:—One or two pairs; seven papillæ in two rows.

F. pardus:—One or three pairs.

F. domestica, *F. sylvestris*, *F. caffra*, *F. viverrina*, *F. nebulosa*, *F. bengalensis*, *F. concolor*:—Two pairs of papillæ.

F. lynx. *F. caracal*, *F. rufa*, *F. pardalis*:—Three pairs of papillæ.

Cynœlurus jubatus:—Two or three pairs of papillæ.

Family Viverridæ.

Viverra civetta:—Three papillæ in a triangle.

„ *fusca*:—Six papillæ in a V.

Civettictis civetta:—Three papillæ in a triangle.

„ „ Five papillæ in a V.

Viverricula malaccensis:—Three papillæ in a triangle.
Genetta felina:—Four papillæ in a V.
„ *pardina*:— „ „ „
„ *tigrina*:—Two papillæ on the right side and one on the left.
Hemigale hardwickii:—Three papillæ in a triangle.
„ „ :—Four „ „ V.
Paradoxurus larvatus:—Three „ „ triangle.
„ *hermaphroditus*:—Three papillæ in a triangle.
„ *typus*:—Five papillæ in a V.
Mungos mungo, *M. ichneumon* (several examples of each species):—Three papillæ in a triangle.
Atilax paludinosus:—A pair of papillæ.
Nandinia binotata, *Suricata tetradactyla*, *Galidia elegans*:—Three papillæ in a triangle in several examples of each species.
Arctictis binturong:—Eighteen papillæ in a double V (text-fig. 15 *h*).
Cynictis penicillata:—Three papillæ in a triangle.
Crossarchus obscurus:— „ „ „ „

Family Hyænidæ.

Hyæna striata:—A pair of papillæ (text-fig. 21).
„ „ :—Two pairs of papillæ.
H. crocuta:—A pair of papillæ.

Family Protelidæ.

Proteles cristatus:—A pair of papillæ (text-fig. 21).

Fungiform Papillæ:—These are numerous or scanty in the Æluroidea; and in some tongues they are well represented, but indistinct. They may stretch right across the dorsum, or they may be absent from the centre, thereby forming a dorsal bounding zone. They are numerous, scanty or absent on the ventral papillary zone. They have the usual arrangement in clusters and rows of varying degrees of obliquity. They are hemispherical or pedunculated, and the surfaces are smooth or granular.

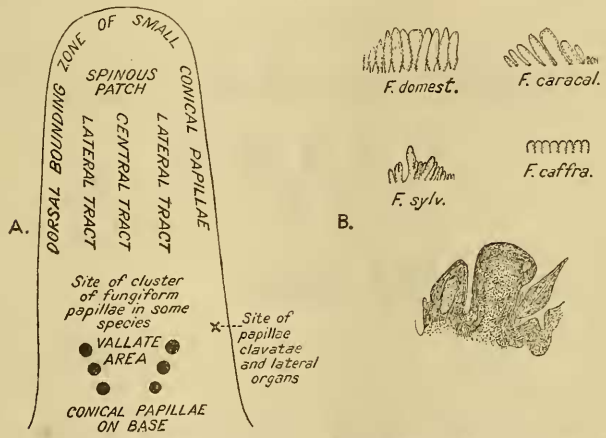
Their distribution on the oral part of the dorsum is determined by the presence or absence, and characters, of the patch of papillæ spinosæ. As a rule they are absent from the latter, but some are present on it in *F. caracal* (text-fig. 20).

In many Carnivora lateral organs are absent, and it is probable that fungiform papillæ lying on the postero-lateral parts of the dorsum replace them. This has been definitely proved to be the case in *Felis domestica*. And it is shown below that club-shaped fungiform papillæ with well-marked taste-buds lie in the position of lateral organs in some Felidæ.

In the Felidæ there may be many fungiform papillæ just behind the apex, but they are never as large and prominent as those in

the Primates. The cluster contains many papillæ in *Felis pardus*, *F. nebulosa*, *F. bengalensis*, *F. concolor*, and *Cynælurus jubatus*. It contains few papillæ in *F. leo*, *F. tigris*, *F. viverrina*, and *F. sylvestris*. No apical fungiforms are present in *F. pardalis*. The fungiforms situated along the sides of the oral part of the dorsum also vary. They are absent in some examples of *F. leo*, moderately developed in *F. sylvestris*, *F. pardalis*, and *F. concolor*, and numerous in *F. pardus*, *F. nebulosa*, *F. viverrina*, *F. bengalensis*, and *Cynælurus jubatus*. No papillæ are present in the spinous patch, except in *F. caracal* (text-fig. 20). On the dorsum behind the spinous patch there are insignificant or prominent fungiform papillæ; they are poorly developed in *F. leo*, *F. tigris*, *F. viverrina*, *F. pardalis*, and *Cynælurus jubatus*; they are present

Text-figure 16.



The divisions of the Æluroid tongue (A.) and the characters of the papillæ clavatæ (B.). *F. domest.*: domestic cat; *F. sylv.*: wild cat; a papillæ with a taste-bud greatly magnified is seen in the lower right-hand corner.

in moderate numbers in *F. pardus*, numerous in *F. nebulosa* and *F. caffra*, and very prominent in *F. sylvestris*.

On the posterior parts of the lateral parts of the dorsum there is sometimes a row of finger-like or clubbed papillæ for which I propose the name of papillæ clavatæ (text-fig. 16 A and B). They lie in the position of the lateral organs, and they appear to be modified fungiform papillæ. Histological examination reveals the presence of taste-buds in their epithelium. They are useful for purposes of classification, being present only in *Felis domestica*, *F. sylvestris*, *F. caffra*, and *F. caracal*. Until material comes to hand I am unable to state whether they occur in *F. chaus* and *F. lynx*. They are relatively largest in *F. caracal*.

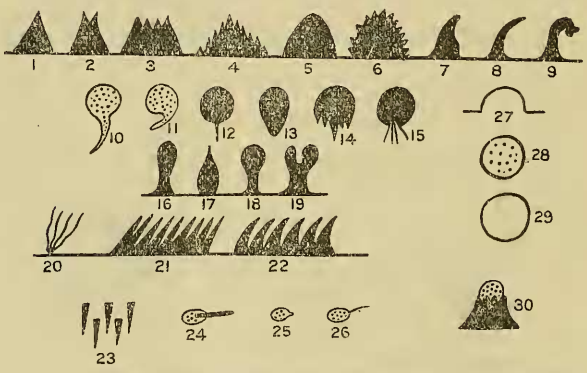
Watson and Young (**33**) stated that the fungiform papillæ are

numerous in *Hyæna crocuta*. In *H. striata* they are not very numerous.

In *Proteles cristatus* (text-fig. 21) the papillæ form a marked cluster in front of the vallate area, and others are all over the dorsum.

In the Viverridæ the conditions of the fungiform papillæ are more varied than in the Felidæ, for the patch of papillæ spinosæ is absent, weak or strong; and the distribution of fungiform papillæ depends on its characters. In *Nandinia binotata* (text-fig. 21), *Viverra civetta*, and *Civettictis civetta* there is no spinous patch, and fungiform papillæ cover the dorsum from the apex of the tongue to the vallate area, and from one side to the other. A few papillæ are present on the ventral papillary zone. In *Paradoxurus larvatus* the patch is small, and its component conical papillæ are slender; fungiform papillæ encircle it, and a

Text-figure 17.



The lingual papillæ seen under a hand-lens. 1–26: conical papillæ; 27–30: fungiform papillæ.

few are found on it. In other species the arrangement of the fungiform papillæ and the patch are as in the Felidæ.

The characters of the fungiform papillæ are shown in text-fig. 17.

No papillæ clavatæ are present in the Hyænidæ, Protelidæ, and Viverridæ.

The value of the clavate and other fungiform papillæ for purposes of classification is shown on page 149.

Conical Papillæ:—As the mechanical function predominates over all others in the Æluroidea, the conical papillæ are strongly developed. And they are provided with sharp-pointed horny sheaths. In the fore part of the oral division of the dorsum there is, in most cases, a patch of large conical papillæ which have been termed papillæ spinosæ; and the area on which they stand is called the spinous patch in this paper (text-fig. 16 A).

The patch may be completely surrounded by a zone of small papillæ, or it may extend laterally till it covers the whole width of the tongue. The histology and chemistry of the horny epithelial sheaths of the papillæ have already been described by Severin (28), Klein and Verson (17), Csokor (7), Podwisotsky (25), and Ranvier (23). The ventral papillary zone may be composed of small conical papillæ alone, or of both conical and fungiform types.

Family Felidæ:—In all forms the spinous patch is surrounded by a zone of small papillæ, but it varies in size, and in the prominence of its papillæ. The points of the papillæ are directed backwards, and are straight or recurved to a variable degree; but those of the papillæ on the encircling zone face backwards and inwards. The lateral papillæ may increase or decrease from before backwards, but the papillæ spinosæ increase in size from without inwards.

In all Felidæ except *F. leo* and *F. onca* the conical papillæ extend back to the epiglottis, but in these species the most posterior papillæ are separated from the epiglottis by a smooth mucous surface. The conical papillæ on the pharyngeal part may be smaller or larger than those on the oral part of the dorsum.

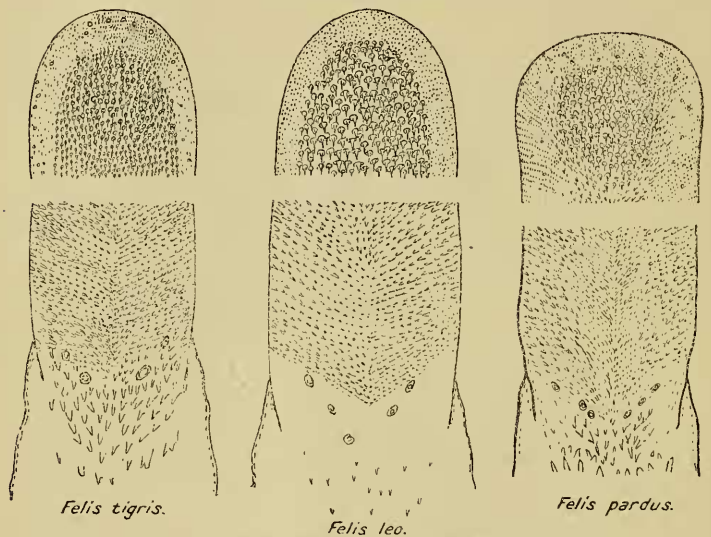
The characters to which special attention must be paid are:—

1. The extent of the small band of conical papillæ encircling the patch of papillæ spinosæ, and the relative quantities of fungiform papillæ situated on it.
2. The posterior limit of the spinous patch, and the distance between the anterior extremity of the patch and the apex of the tongue.
3. The characters of the papillæ spinosæ, particularly the shape of their spines and their closeness or separateness.
4. Characters of the conical papillæ behind the spinous patch.
5. Presence or absence of a row of papillæ clavatæ in the region of the lateral organ on each side.
6. The relative sizes of the conical papillæ on the oral and pharyngeal parts of the dorsum.
7. Character of the ventral papillary zone.

In *Felis leo* (text-fig. 18) the small papillary zone girdling the spinous patch extends back along the anterior third of the tongue. The spinous patch begins close to the apex of the tongue, but does not reach the middle of the oral part of the dorsum. The papillæ spinosæ have sharp, recurved, closely-set points so their bases are not much exposed. Behind the patch the conical papillæ form a central band of small ones and two lateral tracts of large ones. No clavate papillæ are present, and the papillæ on the pharyngeal part of the dorsum are small. In *F. tigris* (text-fig. 18) the conditions are in general similar to those in the lion, but their development is not so great. The papillæ spinosæ have recurved, but not very prominent points, but the conical papillæ on the pharyngeal part of the tongue are prominent. Fungiform

papillæ are more marked behind the spinous patch. The tongue is not separated from the epiglottis by a smooth mucous tract. In *F. sylvestris*, *F. domestica*, and *F. caffra* (text-fig. 20) the zone of small conical papillæ surrounding the spinous patch extends far back along the lateral aspects of the dorsum; it has many fungiform papillæ at the sides of the tongue, but few behind the apex. The spinous patch begins a considerable distance behind the apex of the tongue, and extends to the middle of the oral part of the dorsum. The papillæ spinosæ are discrete, their points are straight, and their granular bases are visible. Papillæ clavatæ are well-marked. The conical papillæ behind the spinous patch are divisible, according to size, into a central and two lateral

Text-figure 18.

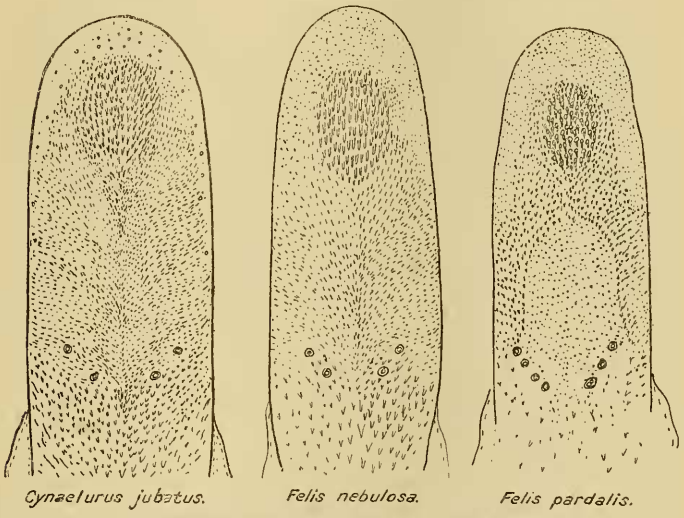


The tongues of the Pantherinæ.

tracts; and the papillæ on the pharyngeal part of the tongue are large. In *F. pardus* (text-fig. 18), of which several varieties were examined, the dorsal bounding zone of small conical papillæ only extends along the apex and anterior third of each lateral aspect of the dorsum; and it is well-studded with fungiform papillæ; it is also very narrow when compared with the zone on other tongues. The spinous patch begins close to the apex of the tongue, but does not reach the middle of the oral part of the dorsum. The papillæ spinosæ are discrete, and have sharp recurved points. No papillæ clavatæ are present. The conical papillæ behind the spinous patch are divisible into a central and two lateral tracts; and the papillæ on the base of the tongue are

large, soft and not very closely aggregated. The tongue of *F. nebulosa* (text-fig. 19) differs somewhat from that of the last species. The wide dorsal bounding zone of small papillæ contains more fungiforms. The spinous patch begins far from the apex of the tongue and reaches nearer the middle of the oral part of the dorsum. In other respects the tongues are similar. In *F. viverrina* the dorsal bounding zone extends along the anterior third of the oral part of the dorsum: it is narrow and has few fungiforms. Clavate papillæ are absent. The spinous patch begins a short distance behind the apex of the tongue, but lies entirely in the anterior third of the tongue. Its constituent papillæ are slender and inconspicuous. The papillæ behind the spinous patch are arranged in a central and two lateral tracts, and the conical

Text-figure 19.



The tongues of the Acinonychinæ and Felinæ (No. 1).

papillæ on the base of the tongue are narrow, pointed, and discrete. In the tongue of *F. bengalensis* the dorsal bounding zone is relatively wide and has well-developed papillæ fungiformes. No papillæ clavatæ are present. The spinous patch begins some distance behind the apex of the tongue and extends to the middle of the oral part of the dorsum; its papillæ have strong points. The central and lateral tracts of papillæ behind the spinous patch are just distinguishable; and the papillæ on the pharyngeal part are long, slender, and discrete. In *F. pardalis* (text-fig. 19) the dorsal bounding zone is narrow and has few fungiform papillæ. The spinous patch does not extend as far back as the middle of the oral part of the dorsum. In other respects it is similar to

that of *F. bengalensis*. In *F. caracal* (text-fig. 20) the bounding zone is wide. The spinous patch is small, and begins far from the apex of the tongue. The conical papillæ behind the patch are divisible, according to size, into a central and two lateral tracts. Papillæ clavatæ are very well marked, and form a row of discrete, prominent structures. The conical papillæ on the base of the tongue are pointed and discrete, being separated by wide areas of the pharyngeal part of the dorsum.

In *Cynœlurus jubatus* (text-fig. 19) the bounding zone extends half-way back along the dorsum, and it lodges a few small fungiform papillæ. The spinous patch begins far from the apex,

Text-figure 20.

The tongues of the Felinæ (No. 2).

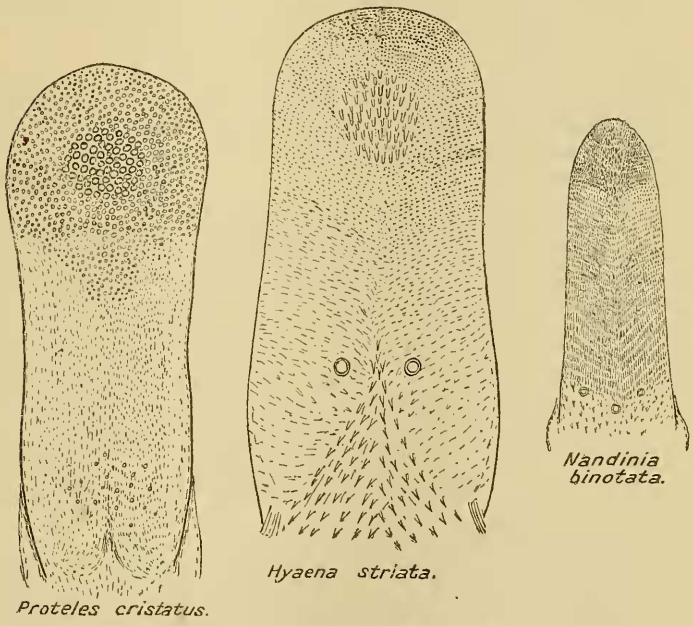
and does not reach the middle of the dorsum; and the points of the papillæ spinosæ are slender and sharp. No papillæ clavatæ are present. The conical papillæ behind the spinous patch are divisible into a central and two lateral tracts, and the conical papillæ on the base are small.

It is, therefore, evident that the tongues of the Felidæ are divisible into two groups, according to the presence or absence of papillæ clavatæ. In the former are *Felis domestica*, *F. sylvestris*, *F. caffra*, and *F. caracal*. As no examples of *F. chaus* and *F. lynx* have come to hand the above list cannot be regarded as complete.

In the latter are *F. leo*, *F. tigris*, *F. pardus*, *F. pardalis*, *F. onca*, *F. serval*, *F. viverrina*, *F. bengalensis*, and *Cynœlurus jubatus*. The subdivision of the Felidæ by other characters is given on page 149.

Family Hyœnidœ:—In *H. striata* the dorsal bounding zone of small papillæ is wide. The spinous patch begins far from the apex, and is less extensive in proportion to the length of the tongue than that of any of the Felidæ; the points of the papillæ spinosæ are small. The division of the conical papillæ behind the patch into central and lateral tracts is not perceptible. The

Text-figure 21.



The tongues of the Hyænidæ, Protelidæ, and Viverridæ (No. 1).

conical papillæ on the base of the tongue are divided into a central band of large elements, and two lateral tracts of small ones. No papillæ clavatæ are present (text-fig. 21).

Family Protelidœ:—The tongue in *Proteles cristatus* is spatular, and the spinous patch covers the whole anterior expanded part (text-fig. 21). The papillæ on the patch are circular or blunt-pointed cones. The conical papillæ behind the patch are very small and are not divisible into central and lateral tracts. Basal conical papillæ are scanty, and no papillæ clavatæ are present.

Family Viverridœ:—The spinous patch is absent, small or well-

developed, and the development of the points varies as shown in the following table:—

Species.	Development of patch.	Development of points.	
Civettictis civetta	−	−	
Viverra civetta	+	+	
Viverricula malaccensis	++	+	
Genetta felina	++	+	
„ *tigrina*	++	+	
Paradoxurus larvatus	+	+	
„ *hermaphroditus*	+	+	
Arctictis binturong	+	+	
Nandinia binotata	−	−	(text-fig. 21).
Mungos ichneumon.....	+	++	
„ *mungo*	++	++	
Atilax paludinosus.....	++	+++	
Galidia elegans	++	+	
Cynictis penicillata	+++	++	
Suricata tetradactyla	+	+	
Crossarchus obscurus	++	+++	(text-fig. 22).

The conical papillæ have the usual direction, and increase in size in the usual manner. They usually lie flat on the lateral borders, but they project from them in *Nandinia binotata* and *Mungos ichneumon*. Behind the spinous patch they are not divisible into central and lateral tracts as in the Felidæ. The conical papillæ on the base of the tongue are usually small, and they are close together or discrete. They are small and discrete in *Nandinia binotata* and *Viverricula malaccensis*; but they are small and close together in *Mungos mungo*, *M. ichneumon*, *Civettictis civetta*, and *Viverra civetta*. They are large in *Paradoxurus larvatus*, *Genetta felina*, *Suricata tetradactyla*, and *Arctictis binturong*.

No papillæ clavatæ are present.

Lateral Organs are poorly developed or absent. Various authors have described them in *Felis domestica* (**19, 17, 7, 12, 31**), *F. tigris* (**19**), *F. pardus* (**12**), *Viverra civetta* (**19**), *V. fusca* (**20**), *Genetta tigrina* (**22**), and *Hyæna striata* (**19**). In my specimens they were arranged as follows:—

Family Felidæ:—Organs absent in *Felis leo*, *F. domestica*, *F. sylvestris*, *F. caffra*, *F. caracal*, *F. bengalensis*, *F. nebulosa*, and *F. pardalis*. They are represented by slight fissures in *F. pardus*, *F. concolor*, *F. viverrina*, and *Cynælurus jubatus*.

Family Viverridæ:—Organs absent in all except *Nandinia binotata*, *Viverra civetta*, *Cynictis penicillata*, and *Suricata tetra dactyla*.

One or two foliate clefts are present in the Hyænidæ and Protelidæ.

Glands:—Lymphoid nodules and the orifices of ducts and pits are scanty or absent on the base of the tongue. No apical gland

of Nuhn is present. In the cat mucous glands predominate over Ebner's glands.

Lytta:—The lytta lies in the free part of the tongue close to the apex. It is short, and thick or slender; and it is not of much mechanical advantage. Oppel describes its histology, and recapitulates the views of Codronchi, Casserius, and Cuvier as to its nature. It has been described in the cat by Flower (**10**) and by Ludwig, Prince of Bavaria (**18**). In *Felis leo* it is three-quarters of an inch long and half an inch thick.

The *ventral surface of the tongue* is plain. It has a well-marked frenum, and there is frequently no trace of a ventral mesial sulcus and ventral papillary zone.

Section Cynoidea.

The form of the tongue and the characters of the apex and lateral borders are essentially similar to those in the Æluroidea. But mesial dorsal sulci are sometimes well marked.

The *circumvallate papillæ* are arranged in converging lines which do not meet in all specimens examined by myself and recorded by others. They are round or oval on plan, and cylindrical or conical on elevation; the fossa is usually well marked, and the vallum is smooth, granular or lobulated. All papillæ may be equal in size, or the members of a row may vary. In some cases the papillæ are concealed by overhanging conical papillæ. The number of papillæ in my specimens, and those in the Museum of the Royal College of Surgeons are:—

Canis familiaris:—One to six pairs.

Canis lupus:—Two or three pairs.

Canis cinereo-argentatus:—Five papillæ in two rows (**31**).

Canis aureus:—One pair.

Canis mesomelas and *C. azaræ*:—Two pairs of papillæ.

Canis thous, *C. occidentalis*, *C. jubatus*:—Three pairs of papillæ.

Vulpes vulpes, *V. bengalensis*, *V. leucopus*, *V. fulvus*, *Alopex lagopus*, *Cyon dukhensis*, *Lycaon capensis*, and *Nyctereutes procyonides*:—Three pairs of papillæ.

As the number of papillæ is variable in those species of which I was enabled to examine several examples they are useless for purposes of classification.

The *fungiform papillæ* may be very obvious, but they are usually minute, and it may be necessary to employ histological examination to detect their presence. In a specimen of *Vulpes leucopus* I was unable to detect them at all. They have the usual arrangement, but the apical cluster is not prominent. Some are present on the ventral papillary zone. Well-developed taste-buds are present in *Canis familiaris* and *Vulpes vulpes*. Papillæ clavatæ are absent.

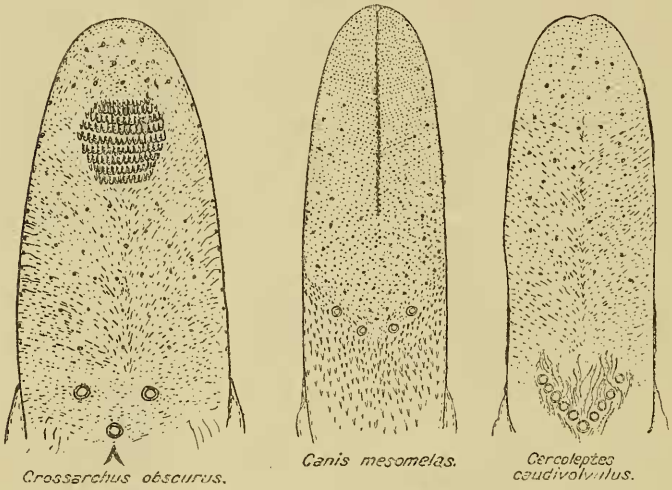
Conical Papillæ:—No spinous patch is present. The papillæ have the usual arrangement in rows and clusters, but those on the oral part are much smaller than those on the pharyngeal

division of the dorsum. A clear line of demarcation, which is concave forwards, separates the two groups. This arrangement was also described in my paper on the tongues of the Lemuroidea (29). The forms are shown in text-fig. 17, 1–6 and 12–15.

Lateral Organs:—Various authors have described them in *Canis familiaris* (23), *C. lupus* (5), *C. cinereo-argentatus* (31), *C. mesomelas* (31), *C. jubatus*, *Vulpes vulpes*, *V. leucopus*, and *V. fulvus*. In *Canis familiaris* they are variable, being present in some specimens, but absent in others. Authors have described the histology of these structures in that species. In the specimens at my disposal I found organs in some specimens of *Canis familiaris*, but not in others.

In the specimens at my disposal I found the organs always very slightly developed when present. No traces were present

Text-figure 22.



The tongues of the Viverridæ (No. 2), Canidæ, and Procyonidæ (No. 1).

in *C. lupus*, *C. mesomelas*, *C. jubatus*, *Vulpes vulpes*, *V. leucopus*, *V. fulvus*. But they were present in all other Canidæ enumerated in this paper.

Glands:—In the dog and common fox serous glands surround the vallate papillæ and lateral organs, and mucous glands cover the base of the tongue. But there is no apical gland of Nuhn. Lymphoid nodules and orifices of ducts and pits are scanty on the base of the tongue.

The frenum is well marked, but there are no traces of frenal lamellæ, plicæ fimbriatæ, and foramen cæcum. The median glosso-epiglottic fold may run forwards for a considerable distance on to the pharyngeal part of the tongue and separate the conical papillæ into two groups.

The lytta is well developed, and its histological characters have been described by many authors, whose observations have been collected by Oppel (23). In *Canis aureus* it is continued to the hyoid bone by a long, slender fibrous thread.

The characters of the tongues of the Cynoidea are so similar in many species that they cannot be used for purposes of classification, as they can in the case of the Æluroidea.

Section Arctoidea.

The tongue is long, narrow and thin. The *apex* is rounded and may or may not have a notch. Notches are absent in the Mustelidæ and Æluridæ, but are well marked in some of the Procyonidæ and Ursidæ. Minute conical papillæ clothe the apex, and the fungiform papillæ in that region are small in the Mustelidæ and Æluridæ. The apical conical papillæ are long and prominent, but the fungiform papillæ are small in the Ursidæ. The apical fungiform papillæ are large, but the conical papillæ are small in the Procyonidæ. The *lateral borders* are acutely or widely rounded, but lateral organs are variable. The conical papillæ thereon lie flat in the Mustelidæ, Æluridæ, and Procyonidæ, but they stand up prominently in the Ursidæ. It was shown in a previous paper (30) that lateral projections are present in *Sus* and the Cetacea. Median *dorsal sulci* are present in many species, but they are very prominent in *Mustela martes*, *M. erminea*, and some species of *Ursus*. Transverse ridges and sulci are very well marked in *Mustela erminea*. The entire dorsum is clothed with papillæ which may be inconspicuous or very prominent, and the conical papillæ on the base may be much larger, or smaller than those on the oral part of the dorsum.

Circumvallate Papillæ :—The following arrangements exist :—

1. One or more pairs of papillæ in two converging rows which do not meet.
2. Several papillæ in V-formation.
3. Several papillæ in a semicircle.

The following list shows the arrangements observed by myself and recorded by others :—

Family Mustelidæ.

Mustela martes :—Two pairs of papillæ.
,, *erminea* :—Three pairs of papillæ in Münch's 27 specimens.
Ictonyx zorilla :—A pair of papillæ.
Putorius vison :—Two pairs of papillæ in three specimens.
Meles meles :—Seven papillæ in a semicircle (text-fig. 23) or five to nine papillæ in a V.
Arctonyx collaris :—Eight papillæ in a V.
Lutra vulgaris :—Five or eight papillæ in a V.
Mephitis mephitica :—A pair of papillæ.
Conepatus proteus :—Five papillæ in a V.
Galictis vittata :—Eight papillæ in a V.

Family Procyonidæ.

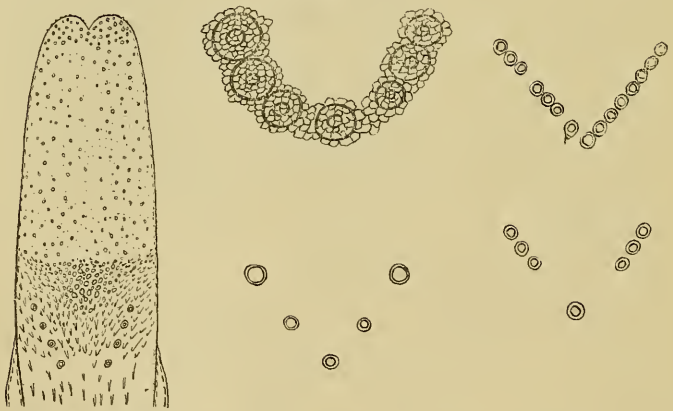
Procyon lotor :—Five pairs of papillæ, or twelve papillæ in a V (text-fig. 23).
Nasua narica :—Four to eight pairs of papillæ in a V (text-fig. 23).
Cercoleptes caudivolvulus :—Ten papillæ in V-formation (text-fig. 22).
Ælurus fulgens :—Ten or twelve papillæ in a V (text-fig. 23).

Family Ursidæ.

Ursus maritimus :—Two pairs of papillæ, or ten papillæ in a V.
,, *arctos* :—16 papillæ in a V.
,, *americanus* :—20 papillæ in a semicircle.
,, *fuscus* :—Ten pairs of papillæ.
,, *malayanus* :—Seven to thirteen papillæ.
,, *labiatus* :—16 or 17 papillæ in a V.
Melursus ursinus :—Ten papillæ in a V.

The papillæ are round or oval on plan and cylindrical or conical on elevation in all except *Meles meles* in which globular forms are present. The vallum is smooth, granular or lobulated, and the

Text-figure 23.



The tongue of *Nasua* and the arrangements of the vallate papillæ in the Mustelidæ and Ursidæ.

fossa is closed or patulous. In a specimen of *Meles meles* (text-fig. 23) the mucosa over the papillæ is brown and tesselated ; but this appearance was absent in five specimens. The vallums may be in contact (text-fig. 23) or separated by intervals. Numerous taste-buds are present.

The *fungiform papillæ* may be just visible to the naked eye, or

they may stand up prominently. They are inconspicuous in *Mustela erminea*, *M. martes*, and some species of *Ursus*. They are small, but obvious, in *Meles meles*, *Lutra vulgaris*, *Arctonyx collaris*, *Galictis vittata*, *Procyon lotor*, and *Ælurus fulgens*. They are larger and more prominent in *Nasua narica* than in any other Carnivore examined by myself. They have the usual arrangement in clusters and rows of varying degrees of obliquity; but they usually stretch from the mid line to the lateral borders of the tongue. Those at the posterior parts of the lateral borders are very prominent in *Cercoleptes caudivolvulus*, and may replace the lateral organs. Taste-buds are present in the fungiform papillæ in many species. Papillæ clavatæ are absent.

Conical papillæ cover the entire dorsum from the apex back to the epiglottis, and they frequently form a ventral bounding zone. But there is no trace of papillæ spinosæ. The conical papillæ have the usual arrangement into apical clusters and rows of varying degrees of obliquity. But their distribution according to size differs considerably as follows:—

1. Papillæ on the oral part of the dorsum large, but those on the pharyngeal part are small:—*Mustela*, *Arctonyx*, *Galictis*.
2. Papillæ on oral part small, but those on the pharyngeal part large:—*Nasua*, *Procyon*, *Ælurus*, *Ursus*, *Melursus*, *Ictonyx*.
3. Papillæ small all over:—*Meles*.
4. Papillæ large all over:—*Lutra*.

The papillæ make the edges of the tongue rough in *Mustela*, *Lutra*, and *Nasua*, but the edges are smooth in *Meles*. In *Ursus* they stand up prominently on the apex of the tongue and the anterior ends of the lateral borders.

Lateral Organs:—There is considerable difference of opinion as to their occurrence in the Arctoidea. Various authors have described them in *Mustela martes*, *Putorius vison*, *Procyon lotor*, *Cercoleptes caudivolvulus*, and several species of *Ursus*. I observed no trace of these structures in *Mustela erminea*, *M. martes*, *M. foina*, *Ictonyx zorilla*, *Mephitis mephitica*, *Conepatus proteus*, *Meles meles*, *Lutra vulgaris*, *Procyon cancrivorus*, *Nasua narica*, *Ælurus fulgens*, *Cercoleptes caudivolvulus*, *Arctonyx collaris*, *Galictis vittata*. Some small foliate clefts were seen in *Procyon lotor*, *Ursus maritimus*, and *Melursus ursinus*.

There is no trace of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum. Lymphoid nodules and the orifices of ducts and pits are scanty on the base of the tongue.

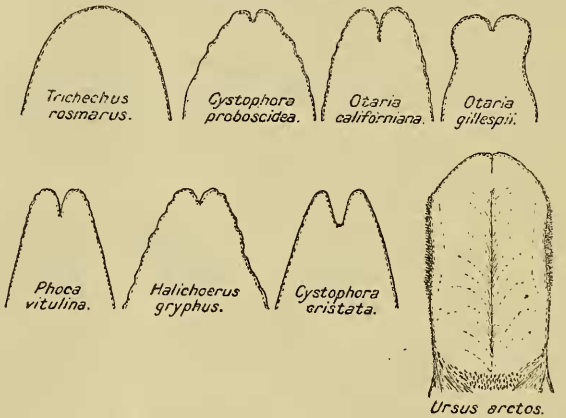
The lytta is present, and it reaches its highest degree of development in *Cercoleptes caudivolvulus*, in which it is long, ligamentous and ensheathed.

Suborder PINNIPEDIA.

The tongues are shorter and wider than those of the Fissipedia, and they taper more rapidly.

The *apex* is entire or cleft, and may be smooth or covered with lobules and papillæ. It is round, massive, smooth, and entire in *Trichechus rosmarus*. In *Cystophora proboscidea* it is rounded, with a deep median cleft, and is covered with coarse lobules. In other forms it has a wide apical sulcus separating its apex into two lateral parts, which vary in appearance. Both halves are covered with papillæ which may be restricted to the apices or extend along the borders. As the specimens examined were not at my disposal for histological purposes I am unable to state whether the papillæ and lobules in the Pinnipedia are homologous with those in the Cetacea and *Galeopithecus*. The halves are rounded in *Otaria californiana*, and they are rounded and laterally projecting in *O. gillespii*. They are sharper in *Phoca vitulina*, *Halichœrus gryphus*, and *Cystophora cristata*.

Text-figure 24.



The tongues of the Pinnipedia and *Ursus*.

The *lateral borders* are rounded in all forms, but are elevated in some examples of *Phoca vitulina*. They are massive in *Trichechus rosmarus* and *Cystophora proboscidea*; they are smooth in the former, but covered with papillæ and lobules in the latter. In other forms they have many small papillæ. In some forms, such as *Otaria californiana*, there are rows of elevations at their posterior extremities, but these must not be mistaken for lateral organs.

Sulci and Ridges:—No ridges are present on either surface. Mesial dorsal and ventral sulci are faint or absent, as in the Cetacea, but transverse sulci were only observed in *Cystophora proboscidea*.

In all forms except *Trichechus rosmarus* the tongue has no intermolar elevation, and the oral part can usually be distinguished

from the pharyngeal division. The former is covered with papillæ in all forms except *Cystophora proboscidea*, and the latter is folded and covered with orifices of glands and pits, as in the Cetacea.

The *circumvallate papillæ* are the chief gustatory organs in *Trichechus rosmarus* and *Cystophora proboscidea*, which have no lateral organs. They are sometimes absent as well, so the gustatory function is poor or absent in some Pinnipedia. The following table shows the arrangement of the papillæ and lateral organs:—

Species.	Circumvallate papillæ.	Lateral organs.
Otaria californiana	Absent.	Absent.
„ *gillespii*	„	„
Trichechus rosmarus	7 in a V.	„
Halichœrus gryphus	Absent.	„
Phoca vitulina	5 in a V.	Well marked.
„ „	10–12 in a V.	„ „
„ „	3 in a triangle.	„ „
„ „	8–9 in a V.	„ „
Cystophora cristata	Absent.	„ „
„ *proboscidea*	8 in a V.	Absent.

It is, therefore, evident that gustatory organs attain their greatest development in *Phoca vitulina*, and they are poorest in *Otaria californiana*, *O. gillespii* and *Halichœrus gryphus*. The conditions are intermediate in *Trichechus* and *Cystophora*.

Fungiform Papillæ:—These are numerous, scanty or absent; and when many are present they are thickly clustered on the centre or sides of the dorsum, or spread all over it. They are hemispherical or pedunculated, and the surfaces are smooth or granular.

Papillæ are absent in *Halichœrus gryphus*. They are numerous, especially on the centre of the oral part of the dorsum, in *Cystophora cristata*, but they are aggregated around the edges of the dorsum in *Trichechus rosmarus*. In *Otaria californiana* they are scanty, they stretch right across the dorsum, and they have the usual arrangement. In *Phoca vitulina* the usual mammalian arrangement is present. In the Cetacea fungiform papillæ are absent.

Conical papillæ are absent in *Trichechus rosmarus* and *Cystophora proboscidea*, but they are present in all other forms. And they have their usual arrangement in clusters and rows on the oral part of the dorsum. They also increase in size in the usual manner from before backwards and without inwards. The pharyngeal part is folded and devoid of papillæ standing up from the surface in *Cystophora*, *Phoca*, and *Halichœrus*, but large

pedunculated or tapering papillæ are present in *Trichechus*, *Otaria californiana* and *O. gillespii*.

No papillæ clavatæ are present in the place of lateral organs.

Glands:—The orifices may be numerous, scanty or absent. In *Trichechus rosmarus* they are thickly clustered on the oral part of the dorsum, but in other forms they are mainly present on the pharyngeal part.

The frenum is slight or absent, and there are no traces of frenal lamellæ, sublingua, plicæ fimbriatæ, or foramen cæcum.

The ventral papillary zone is narrow in *Otaria* and *Cystophora*.

Tuckerman (**31**) described how many fat cells are present in the mucous membrane, submucous tissue, and subpapillary zone in *Phoca vitulina*.

No lytta is present in the specimens of *Phoca vitulina* and *Otaria californiana* examined by myself. And the median glosso-epiglottic fold is well marked in the former, but absent in the latter.

The comparisons between the tongues of the Fissipedia and Pinnipedia are shown in the following scheme:—

Suborder Fissipedia:—Tongues long, narrow, thin. Apex entire. Few have laterally-projecting papillæ on margins. Pharyngeal part not folded. Vallate papillæ always present. No gland orifices seen on oral part. Frenum and lytta present. Spinous patch and papillæ clavatæ sometimes present. Lateral organs variable.

Suborder Pinnipedia:—Tongue shorter, wider, thicker. Apex cleft in all except *Trichechus*. Edges lobulated or have laterally-projecting papillæ. Mucosa of pharyngeal part folded. Many glandular orifices present. Vallate papillæ frequently absent. Lytta absent. Frenum slight. No trace of a spinous patch or papillæ clavatæ. Lateral organs variable.

Systematic.

When the characters described above are arranged in systematic order the following results are obtained:—

Suborder FISSIPEDIA.

Section Æluroidea.

Spinous patch present in all Hyænidæ, Felidæ, Protelidæ, and most Viverridæ.

Family Felidæ:—Conical papillæ behind spinous patch divided into central and lateral tracts. Patch never reaches edges of tongue. Basal conical papillæ never form a median strip.

Family Viverridæ:—Conical papillæ behind the patch not divided into central and lateral tracts. Spinous patch never

reaches edges of tongue. Basal conical papillæ never form a median strip.

Family Hyænidæ:—Conical papillæ behind spinous patch not divided into central and lateral tracts. Patch never reaches edges of the tongue. Basal conical papillæ form a prominent central strip.

Family Protelidæ:—Conical papillæ behind spinous patch not divisible into central and lateral tracts. Patch reaches margins of tongue. Basal conical papillæ never form a median strip.

Family Felidæ.

A. Spinous patch begins close to apex of tongue, and is restricted to the anterior part of the dorsum. Papillæ spinosæ have recurved points. No papillæ clavatæ.

i. Tongue separated from epiglottis by a long, smooth tract of mucous membrane ..... *Felis leo, F. onca.*

ii. Tongue not separated from epiglottis by a long. smooth mucous tract.

a. Papillæ spinosæ weak ..... *F. tigris.*

b. Papillæ spinosæ strong ..... *F. pardus.*

B. Spinous patch begins close to apex of tongue and reaches middle of oral part of dorsum. Points of papillæ spinosæ recurved and strong. Basal conical papillæ moderately large or small. No papillæ clavatæ.

i. Basal conical papillæ moderately long and close ..... *F. yaguarundi.*

ii. Basal papillæ small and discrete ..... *F. concolor.*

C. Spinous patch begins far from apex of tongue. Papillæ spinosæ have strong, straight points. Papillæ clavatæ present.

a. Fungiform papillæ on spinous patch ..... *F. caracal.*

b. No fungiform papillæ on patch.

i. Large fungiforms behind patch ..... *F. sylvestris.*

ii. Small fungiforms behind patch ..... *F. caffra, F. domestica.*

D. Spinous patch begins far from the apex of tongue. Papillæ spinosæ have strong, straight points. No papillæ clavatæ.

a. Basal conical papillæ scanty or absent ..... *F. pardalis.*

b. Basal conicals long, sharp, discrete ..... *F. viverrina, F. bengalensis.*

c. Basal conicals large and close ..... *F. nebulosa.*

E. Spinous patch begins far from apex of tongue. Papillæ spinosæ have slender points. No papillæ clavatæ. Basal conicals numerous, minute, close ..... *Cynælurus.*

Pocock's classification (24) agrees with the above as follows:—

Subfamily Pantherinæ = Group A.
„ Felinæ = Groups B, C, D.
„ Acinonychinæ = Group E.

As regards the Hyænidæ and Protelidæ the characters given at the beginning of this section are all that can be obtained from the tongue for purposes of classification. And the lingual

characters do not show any affinity between *Proteles* and the Hyænas. Moreover, they do not show that *Proteles* resembles any of the Herpestine Viverridæ as stated by Weber.

Family Viverridæ.

A. Spinous patch absent or moderately developed.
  a. Patch absent.
    i. Conical papillæ on oral part of tongue strong, but those on base moderately developed ..... *Nandinia*.
    ii. Conicals on oral part small, those on base strongly developed ..... *Civettictis*.
    iii. Conicals on oral part strong, those on base weak or absent *Viverra*.
  b. Patch slight ..... *Paradoxurus*
  c. Patch moderately developed, and its papillæ are nodular..... *Viverricula*.
  d. Patch moderate, papillæ pointed.
    i. Vallate papillæ in a single V..... *Genetta*.
    ii. Vallates in a double V..... *Arctictis*.
B. Spinous patch strongly developed.
  a. Points of papillæ sharp ..... *Cynictis, Mungos, Atilax*.
  b. Points broad and blunt ..... *Crossarchus*.
  c. Papillæ globular ..... *Suricata*.

Weber divided the Viverridæ into Viverrine and Herpestine subfamilies. The former corresponds to Group A, and the latter to Group B in the above scheme.

Section Cynoidea.

No trace of a spinous patch in any species. Circumvallate papillæ always in converging rows which do not meet. Fungiform papillæ insignificant. Conical papillæ on oral part of tongue small, but those on pharyngeal part large. Characters so similar in all species that they cannot be used for purposes of classification.

Section Arctoidea.

No spinous patch. No papillæ clavatæ. Fungiform papillæ more obvious than in Cynoidea. Conical papillæ variable.

A. Conical papillæ on oral part of dorsum large, but those on pharyngeal part small ... . *Mustela, Arctonyx, Galictis*.
B. Conical papillæ all small from apex of tongue back to epiglottis. *Meles*.
C. „ „ „ large „ „ „ „ „ *Lutra*.
D. „ „ on oral part of dorsum small, but those on pharyngeal part large.
  i. Conical papillæ on anterior ends of lateral borders stand out prominently..... *Ursus*.
  ii. Conical papillæ on anterior ends of lateral borders do not stand out prominently.
    a'. Fungiform papillæ on posterior parts of lateral borders immense. Lytta very large ..... *Cercoleptes*.
    b'. Fungiform papillæ large all over ..... *Nasua*.
    c' „ „ small „ „ ..... *Procyon, Ælurus*.

Suborder PINNIPEDIA.

A. Apex entire. Posterior part of tongue elevated. Fungiform papillæ aggregated round edges of dorsum ..... *Trichechus.*

B. Apex cleft. Posterior part of dorsum not elevated. Fungiform papillæ not aggregated round edges of dorsum.

a. Halves of apex rounded and blunt. No vallate papillæ nor lateral organs. Large pedunculated conical papillæ on base of tongue ..... *Otaria.*

b. Halves of apex sharper. Vallate papillæ or lateral organs or neither present. No large pedunculated papillæ on base.

i. No fungiform papillæ. No vallate papillæ. No lateral organs ..... *Halichœrus.*

ii. Fungiform papillæ, vallate papillæ, and lateral organs well marked ..... *Phoca.*

iii. Fungiform papillæ present. Vallate papillæ or lateral organs present ..... *Cystophora.*

It is, therefore, evident that *Phoca* has a fuller complement of gustatory organs than all other Pinnipedia described above.

Comparisons with the Cetacea.

It is now believed that the Cetacea have affinities with the Arctoidea and Pinnipedia, so it is necessary to compare the tongues. A full description of the Cetacean tongue is contained in the previous paper of this series (**29**).

The tongue is long, narrow and thin in the Arctoidea, but wider and thicker in the Pinnipedia and Cetacea. The *apex* is entire in most Arctoidea and all Cetacea, but is deeply cleft in all Pinnipedia except *Trichechus*. The *lateral borders* have papillæ in the Arctoidea; they are lobulated in the Pinnipedia and Odontoceti, but entire in the Mystacoceti. *Vallate papillæ* are present in all Arctoidea, many Pinnipedia, but no Cetacea. *Conical papillæ* are present in all Arctoidea and most Pinnipedia, but they are scanty or absent in the Cetacea. *Lateral organs* are variable in the Arctoidea and Pinnipedia, but they are absent in all Cetacea. The *orifices of glands* are innumerable in the Cetacea, fewer in the Pinnipedia, and scanty in the Arctoidea. The *frenum* is well marked and the *lytta* is present in the Arctoidea, but the former is slight and the latter is absent in the Pinnipedia and Cetacea. The *lingual fat* is well developed in the Mystacoceti, in smaller quantity in the Odontoceti and Pinnipedia, and very scanty in the Arctoidea. The *lingual muscles* are well developed in the Arctoidea and Pinnipedia, but they are poor in the Cetacea.

It is, therefore, evident that the tongues of the Arctoidea differ markedly from those of the Cetacea, but the conditions are intermediate in complexity in the Pinnipedia. The conditions in the Cetacea are a mixture of degeneration and hypertrophy. The mechanical and gustatory organs have almost disappeared, but the glands have increased. And the pharyngeal glands are very numerous as well. The secretion of these glands

may contain a viscid or glairy substance which protects the mucous membrane from being injured by prolonged immersion in the water. I also observed numerous pits on the roof of the mouth and on the tongue in fresh-water and marine fishes. But they are not so numerous in the Pinnipedia, as might be inferred from a comparative study of the habits of these groups of animals. Poulton (**26**) believes that the large glands in the bill of *Ornithorhynchus* secrete a substance which protects the delicate integument. The glands may also be numerous in the Cetacea because salivary glands are absent.

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